SEASONAL DISTRIBUTION OF SIBLING HAKES, UROPHYCIS CHUSS AND U. TENUIS (PISCES, GADIDAE) IN NEW ENGLAND^{1,2}

JOHN A. MUSICK³

ABSTRACT

The seasonal distribution patterns of sibling hakes, *Urophycis chuss* and *U. tenuis*, differ from one another in depth and geographic area and within each species by life history stage.

Urophycis chuss spawns off southern New England in depths of less than 60 fm and probably at temperatures between 5° and 10°C. Two major spawning concentrations occur, one east of Block Island, the other on the southwest part of Georges Bank. Spawning in the Gulf of Maine probably occurs inshore at depths shoaler than 30 fm. After spawning, the adult fish disperse and the larger individuals move offshore into water 60 fm or deeper where the mature fish remain until the following spring. Juvenile U. chuss are inquiline within sea scallops, Placopecten magellanicus, until they outgrow their hosts or until water temperatures, colder than about 4°C, either kill the hake or force them to seek out warmer temperatures in deeper water. Immature U. chuss remain in the vicinity of the scallop beds if water temperatures are compatible until the fish are in their second year of life. During that autumn, the fish migrate inshore to within 30 fm and remain until water temperatures drop to about 4°C, at which time they move to warmer, deeper water along the offshore shelf. The following spring, these fish migrate inshore with the older adult fish during April and by summer are mature and attain the typical seasonal behavior of adults. Immature U. tenuis in the Gulf of Maine occur at all depths but tend to remain in shallower water than the adults during the winter. Mature U. tenuis migrate inshore in the northern Gulf of Maine in the summer, disperse in the fall, and move into the deepest area of the Gulf in winter. Along the eastern edge of Georges Bank and west of there, both immature and mature U. tenuis are fish of the continental slope. Both stages occur over the shelf in small numbers, but at all seasons the highest concentrations are found deeper than 100 fm. The distribution patterns of these two sibling species are not coincidental, as assumed in the past. Rather, they are complementary. Urophycis chuss is more abundant in the Mid-Atlantic Bight, whereas U. tenuis is more abundant on the Scotian shelf, in the Gulf of St. Lawrence, and on the Grand Banks. They occur together most often in the Gulf of Maine. But even there, U. chuss is more abundant in the southwest sector and *U. tenuis* predominates in the northern part and in the Bay of Fundy.

The geographical ranges and seasonal movements of the red hake, *Urophycis chuss* (Walbaum), and of the white hake, *U. tenuis* (Mitchill), have not been defined because previous workers have had difficulty in distinguishing between the two species (Musick, 1973). The purpose of the present paper is to examine the validity of published accounts of the ranges of *U. chuss* and *U. tenuis*; to compare the seasonal distribution of the two species with regard to depth, bottom temperature, and substrate in New England waters; and to determine whether the patterns of seasonal distribution vary among juvenile, immature, and adult stages (these stages are defined below).

Two recent faunal works treat both species together and give the northern limit of distribution of *U. chuss* and *U. tenuis* as Labrador (Leim and Scott, 1966) or the Grand Banks of Newfoundland (Bigelow and Schroeder, 1953). However neither documentation nor voucher specimens are available to establish the presence of U. chuss off Labrador or on the Grand Banks (as there are for *U. tenuis*). Kendall (1909) reported *U. tenuis* from Labrador, and the Newfoundland Fisheries Research Commission (1932, 1933, 1934) captured U. tenuis along the southwestern edge of the Grand Banks during warmer months of the year. Templeman (1966) reported that all Urophycis taken commercially on the Grand Banks have been U. tenuis (1966) and that he had never seen a specimen of *U. chuss* from Newfoundland waters (pers. comm.). Jordan and Evermann (1898) and Breder (1948) gave the

 $^{^{\}rm 1}$ Contribution Number 562 of the Virginia Institute of Marine Science.

² This paper contains parts of a Ph.D. dissertation submitted to Harvard University.

³ Virginia Institute of Marine Science, Gloucester Point, VA 23062.

FISHERY BULLETIN: VOL. 72, NO. 2, 1974.

northern limit of *U. chuss* as the Gulf of St. Lawrence, apparently on the basis of reports of U. chuss (under the name of Phycis americanus (Block and Schneider)) from the Gulf of St. Lawrence by H. R. Storer (1850), Fortin (1863), Knight (1866), and Gilpin (1867). These authors, however, had followed the nomenclatural usage of D. H. Storer (1839, 1846, 1858) whose descriptions of Phycis americanus from Massachusetts obviously referred to *U. tenuis* because of the large size of his specimens (Musick, 1973). Similarly all other reports of *U. chuss* from the Gulf of St. Lawrence are based on nomenclatural errors or were made by workers (Cox, 1905, 1921; Cornish, 1907, 1912; Craigie, 1916, 1927; Vladykov and Tremblay, 1935; Vladykov and McKenzie, 1935; Mc-Kenzie, 1959; and Vladykov and McAllister, 1961) who by their own admission or by the species descriptions they published had shown their inability to distinguish between U. chuss and U. tenuis (Musick, 1969).

Urophycis chuss is absent from or very rare in the Gulf of St. Lawrence. Several thousand specimens of Urophycis examined at Souris, Prince Edward Island, in August 1966 were all U. tenuis (Musick, 1973). Juvenile and postlarval Urophycis captured in the Gulf of St. Lawrence by Fisheries Research Board of Canada personnel from St. Andrews, New Brunswick, and sent to me for identification were all U. tenuis. Several hundred Urophycis examined on a cruise of the RV Prince in the Northumberland Straits and Magdalen shallows in September 1972 were all U. tenuis (K. Able, pers. comm.).

The Newfoundland Fishery Research Commission captured one *U. chuss* (a pelagic juvenile) and many U. tenuis (benthic adults) on the Scotian shelf between Sable Island and Banquereau Banks (Newfoundland Fisheries Research Commission, 1932). Similarly, trawl collections made from RV Albatross IV on the Scotian shelf in March 1969 and 1970 and November 1969 (J. McEachran, pers. comm.) contained few U. chuss and many U. tenuis. Trawl collections made from RV Cameron between Canso, Nova Scotia, and Banquereau Bank in August 1970 and 1971 contained very few U. chuss but many U. tenuis (C. Wenner and J. McEachran, pers. comms.). To my knowledge the most northeastern locality from which voucher specimens of U. chuss are available is lat. 43°39'N, long. 59°26.5'W (Virginia Institute of Marine Science lot No. 01957) collected by otter trawl from RV

Cameron, 14 July 1971, at a depth of 197 m. Both *U. chuss* and *U. tenuis* have been reported frequently from the Gulf of Maine and the Mid-Atlantic Bight as far south as Cape Hatteras, N.C. (Musick, 1969).

Svetovidov (1955) classified *Phycis borealis* Saemundson 1913, an Icelandic form, as a junior synonym of U. tenuis. Icelandic specimens examined during my study confirm Svetovidov's taxonomic judgment and document the range extension of the species to Iceland. Similarly Bullis and Thompson (1965) reported U. tenuis from the continental slope of the east coast of Florida. I examined these specimens and confirm their identification as U. tenuis.

Fraser-Brunner (1925) reported two small specimens of *U. chuss* from the Irish Atlantic slope but was not certain of their identity: "Two small specimens [25 and 55 mm standard length] apparently referable to this species (*U. chuss*) were taken in the tow net near the surface" *Urophycis chuss* of this size were considered to be unidentifiable by American workers such as Bigelow and Welsh (1925) who had many opportunities to examine small specimens. It is probable that Fraser-Brunner's postlarvae were a species of *Phycis*, not *Urophycis*.

The known ranges of the two species can now be summarized: *U. chuss* occurs on the continental shelf from southern Nova Scotia to North Carolina and may stray to the Gulf of St. Lawrence. *Urophycis tenuis* occurs on the continental shelf and slope from Iceland, Labrador, and the Grand Banks of Newfoundland to the coast of North Carolina, straying as far south as Florida in deep water.

Sampling Procedures

Data for a study of the seasonal distribution patterns of *U. chuss* and *U. tenuis* were collected during a groundfish survey conducted by the National Marine Fisheries Service at Woods Hole, Mass. The survey consisted of nine seasonal cruises by RV *Albatross IV* from the mouth of the Bay of Fundy to Hudson Canyon. Approximately 1,800 fishing stations were occupied, and cruises were conducted during the summer and fall in 1963, 1964, and 1965 and during the winter in 1964, 1965, and 1966.

The survey area was divided into 42 sampling strata according to depth (Figure 1), and stations were located randomly within strata. A No. 36

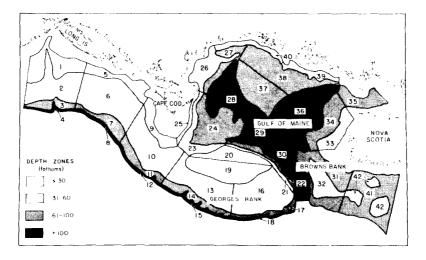


FIGURE 1.—Sampling strata where collections were made during the RV Albatross IV groundfish surveys. (After Grosslein, 1969.)

Yankee otter trawl with a cod-end liner (mesh diameter one-half inch stretched) was towed on the bottom for one-half hour at each station. Towing speed was approximately 3.5 knots. The sampling method and design were described in detail by Grosslein (1969). Length of specimens reported in the present paper is total length unless noted otherwise.

Factors Analyzed

Life History Stages

The following summary of the life histories of U. chuss and U. tenuis is extracted from Musick (1969). Urophycis chuss has pelagic eggs and pelagic larvae that descend to the bottom at a length of about 35 to 40 mm. The young then live within the mantle cavity of the sea scallop, Placopecten magellanicus. The largest U. chuss thus far found inside Placopecten have been 130 to 140 mm long. Urophycis chuss becomes mature at about 290 mm in length. The otter trawl used in the present study catches no eggs or larvae and very few pelagic juveniles; therefore, the life history of *U. chuss* was divided into three demersal stages defined by length: juvenile, \leq 14 cm; immature, 15-28 cm; and mature, \geq 29 cm. Urophycis tenuis has pelagic eggs and pelagic larvae which migrate to the bottom at a length of about 80 mm (or smaller sizes in shallow harbors and estuaries). Urophycis tenuis grows much larger than *U. chuss* and matures at about 500 mm in length. The life history can be divided into only two stages by length in the present study because of the notable lack of young fish in the trawl collections: immature, 9-50 cm; and mature, \geq 51 cm. The biology of these species does not change abruptly in all individuals at a certain size. The size range over which major biological changes occur may be quite broad in populations of these *Urophycis*, but most of the individuals in the population within the size ranges cited above are also within the corresponding ontogenetic stage. By classifying individuals into life history stage by size, it is possible to use length-frequency data to determine whether the geographical distribution patterns of species change during ontogeny.

Natural Divisions of the Study Area

The survey region was divided into two natural subareas according to topography and hydrography. The southern New England subarea includes sampling Strata 1 to 19, i.e., the southern parts of Georges Bank, Nantucket Shoals, and the Mid-Atlantic Bight as far south as Hudson Canyon. The Gulf of Maine subarea includes sampling Strata 20 to 40, i.e., the Gulf of Maine including the northern edge of Georges Bank and Browns Bank (Figure 1).

Topography

The southern New England subarea is characterized by a broad, shallow continental shelf

that slopes gently seaward to about the 100-fathom (fm) isobath, the point sometimes designated as the shoreward limit of the continental slope. The slope itself declines much more steeply to the abyssal plain below. The distance between the 100- and 1,000-fm isobaths is 17 miles off New York City, 16 miles off Martha's Vineyard, and no more than 20 miles along the southern edge of Georges Bank. The width of the continental shelf "out to" the 100-fm isobath is 104 miles off New York City and 76 miles off Martha's Vineyard. Most of the southern New England subarea is contained within the 60-fm isobath.

The Gulf of Maine is a basin of irregular relief within the continental shelf, surrounded by a shallow sill formed by Georges Bank on the southeast, Browns Bank on the east, and the Seal Island Banks on the northeast. The sill in turn is pierced by three narrow channels, which have been named according to their locations: the Great South Channel, 40 fm maximum depth; the Eastern Channel, 128 fm maximum depth; and the Northern Channel, 65 fm maximum depth. Most of the Gulf of Maine is deeper than 60 fm, and the central Gulf, occupied by a Y-shaped trough, is deeper than 100 fm. The topography of the Gulf of Maine has been discussed in detail by Bigelow (1927).

Temperature

The following description of seasonal thermal regimes is compiled from Bigelow (1927, 1933) and original data collected during the Albatross IV surveys. The southern New England subarea has extreme seasonal temperature changes related to its shallowness. Bottom temperatures reach an annual minimum in late February or early March, and are lowest in the shoal waters close to shore and on Georges Bank and highest at the edge of the continental shelf (Figure 2). Spring warming proceeds most rapidly in the shallowest water. By early summer, thermal stratification occurs and prevents the bottom water from warming at intermediate depths (20 to 60 fm) which remain at 4° to 8°C (cooler than both the shoaler depths inshore and the deeper slope water offshore) (Figure 3).

Bottom temperatures in shallow areas attain the annual maximum by the beginning of fall. However, in intermediate depths the maximum is not reached until the thermocline is broken down, usually during October or November



FIGURE 2.—Average winter bottom temperatures compiled from RV *Albatross IV* groundfish surveys 64-1, 65-2, 65-4, and 66-1.

(Figure 4). Winter cooling proceeds more rapidly in shoal water than at intermediate depths. Depths beyond 60 fm under the influence of slope water have relatively little fluctuation in bottom temperatures throughout the year.

In the Gulf of Maine, seasonal thermal changes on the bottom are most pronounced in the shoaler areas. Also, the banks on the Nova Scotian shelf are generally cooler by a few degrees than those to the west, because of the influence of the cold coastal current. Bottom temperatures over most of the Gulf are more stable than those off southern New England, because the deeper Gulf water is made up in part of warm moderating slope water which enters by way of the Eastern Channel.

Procedures of Analysis

Life History Stage by Sampling Strata

An analysis was performed to determine geographical and bathymetric distribution of U. chuss and U. tenuis by life history stage and season. Taylor (1953), Moyle and Lound (1960), and Roessler (1965) demonstrated that fish are not randomly distributed, but that the sampling distribution of the number of individuals of a species taken per sample in a series of collections is contagious and may be best approximated by the negative binomial distribution. The natural log transformation $Y = \ln{(x+1)}$, where x represents the number of individuals of a species taken at each station, tends to "normalize" the negative binomial distribution and substantially

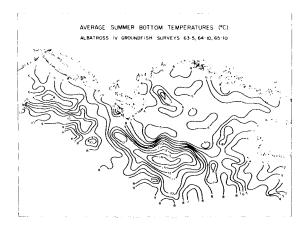


FIGURE 3.—Average summer bottom temperatures compiled from RV Albatross IV groundfish surveys 63-5, 64-10, 65-10.

reduces correlation between the mean and the variance (Pereyra, Heyamoto, and Simpson, 1967). An index of numerical abundance of U. chuss and *U. tenuis* was computed for each stratum by applying the above logarithmic transformation to each catch and calculating the transformed mean catch per stratum. Catch data from all 3 yr were pooled by season of collection, because U. tenuis did not occur frequently enough or in large enough numbers to allow calculation of reliable estimates of mean abundance in some strata on the basis of single cruises. Thus the analysis estimates average seasonal distribution for a 3-yr period probably with little distortion because hydrographic conditions in the principal areas of hake concentration did not differ drastically among the 3 yr.

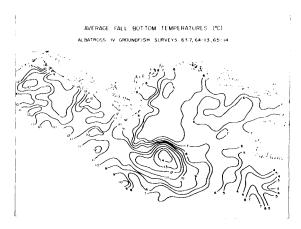


FIGURE 4.—Average fall bottom temperatures compiled from RV Albatross IV groundfish surveys 63-7, 64-13, and 65-14.

Analysis of Temperature and Distribution

The mean catch per tow at each 1°C temperature interval was computed by species, life history stage, subarea, and season. A few temperature intervals were not sufficiently sampled to provide reliable estimates of mean abundance.

RESULTS AND DISCUSSION

Seasonal Distribution of U. chuss

Juvenile (≤ 14 cm) *U. chuss* were rarely captured during summer cruises because young-ofthe-year were pelagic and unavailable to the trawl, and most yearlings had grown larger than 14 cm and were classified as immature fish (Figure 5). In the fall juvenile U, chuss were most abundant off southern New England at depths shoaler than 60 fm (Figure 6). Their distribution coincides with that of the sea scallop, Placopecten magellanicus, which serves as a host to the young inquiline *U. chuss* (Musick, 1969). The shoreward distribution of *Placopecten* is limited by temperature off southern New England. Dickie (1958) found the upper lethal range to be 20° to 23.5°C, temperatures which occur normally in the summer in the shallow bays and sounds of southern New England. In the cooler Gulf of Maine, *Placopecten* are most abundant in inshore areas shoaler than 30 fm and occur commonly in shallow bays (Dow and Baird, 1960; Bourne, 1964). Thus in the Gulf of Maine, the

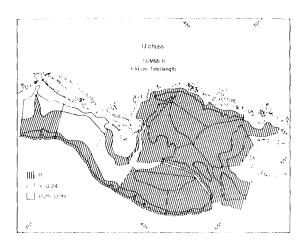


FIGURE 5.—Distribution and abundance of juvenile *Urophycis* chuss during the summer. Abundance in each sampling stratum is indicated on a log scale.

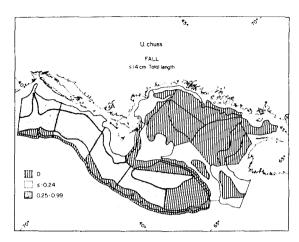


FIGURE 6.—Distribution and abundance of juvenile *Urophycis* chuss during the fall. Abundance in each sampling stratum is indicated on a log scale.

Placopecten habitat (the *U. chuss* nursery) was not sampled because no strata were shallower than 30 fm; consequently estimates of juvenile hake abundance were low.

Juvenile *U. chuss* appear to avoid water colder than 4°C (Figure 7). In winter (Figure 8), abundance of juvenile U. chuss increased in the Gulf of Maine probably because the temperature on the inshore Placopecten beds had dropped below 4°C, prompting the young U. chuss to migrate into deeper water where they became available to our sampling gear. Juvenile U. chuss were absent in winter from the shoaler Georges Bank strata where bottom temperatures were below 4°C. The winter temperature histogram for the Gulf of Maine shows juvenile *U. chuss* to be fairly abundant at 3°C (Figure 7). This apparent contradiction to the rest of the data is attributable to a single large trawl catch at 3°C. The winter distribution pattern of juvenile U. chuss off southern New England was similar to the fall pattern (Figure 8). Abundance values were lower, probably because of natural mortality and growth of some juveniles beyond 14 cm in length.

During the summer, immature (15 to 28 cm) *U. chuss* were abundant from the southern part of Georges Bank throughout the southern New England area at depths of 60 fm or less. Almost no immature fish were taken at depths of 100 fm or more off southern New England (Figure 9). Fish were most abundant at depths of 30 fm or less between Martha's Vineyard and Long Island (Stratum 5). In the Gulf of Maine, the heaviest

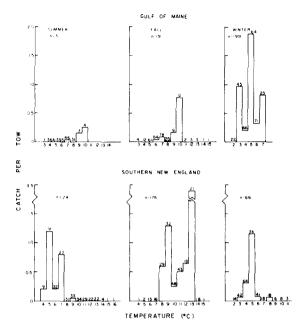


FIGURE 7.—Seasonal catch per tow of juvenile *Urophycis* chuss taken off southern New England and the Gulf of Maine. Abundance data are stratified by temperature intervals of one degree (C). The total number of individuals captured during each season = n. The number of stations occupied at each temperature is indicated above each respective histogram bar.

concentrations of fish were found in the Great South Channel (Stratum 23). Moderate numbers were taken in the deeper strata to the north of the channel area and in shoal water on Georges Bank.

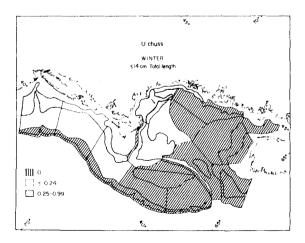


FIGURE 8.—Distribution and abundance of juvenile *Urophycis* chuss during the winter. Abundance in each sampling stratum is indicated on a log scale.

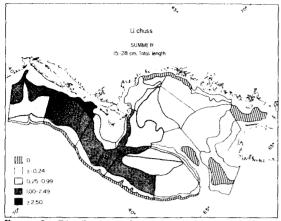


FIGURE 9.—Distribution and abundance of immature *Urophycis chuss* during the summer. Abundance in each sampling stratum is indicated on a log scale.

The fall distribution pattern off southern New England (Figure 10) suggests a movement inshore which is further substantiated by an increase of *U. chuss* in the inshore industrial fisheries landings in October and November (Edwards and Lux, 1958; Edwards, 1958a, 1958b; Edwards and Lawday, 1960). Edwards (pers. comm.) has noted that this fall fishery off southern New England landed mostly small hake. Also reports by Smith (1898) for Woods Hole; Latham (1917) for Orient, Long Island; Breder (1922) for Sandy Hook Bay; and Hildebrand and Schroeder (1928) for the New Jersey coast and New York Bay document an immigration of *U. chuss* in these inshore areas in the fall with an emigration in the winter.

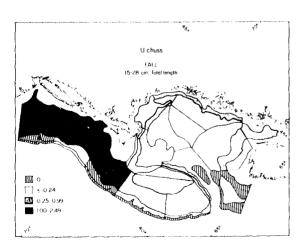


FIGURE 10.—Distribution and abundance of immature *Urophycis chuss* during the fall. Abundance in each sampling stratum is indicated on a log scale.

In the Gulf of Maine, immature *U. chuss* were moderately abundant in the fall around the entire perimeter in strata shoaler than 60 fm.

The winter distribution of immature $U.\ chuss$ was essentially limited to those strata deeper than 30 fm off Long Island, 60 fm off Nantucket, and 100 fm along the southern edge of Georges Bank (Figure 11). In the Gulf of Maine immature $U.\ chuss$ were moderately abundant in strata deeper than 60 fm. Concentrations occurred between 60 and 100 fm along the northern edge of Georges Bank and off Massachusetts Bay and Jeffries Ledge (Stratum 27). The only strata shoaler than 60 fm with moderate values of abundance were 26 and 40, located in the southwestern part of the Gulf where temperatures were warmer than to the north and east.

Immature U. chuss were taken during three seasons within the entire temperature range with the exception of the highest intervals (15° to 16°C), which were inadequately sampled (Figure 12). Most immature fish were taken between 5° and 13°C. As with the juveniles, immature U. chuss were absent from the shallow parts of Georges Bank during the winter and they may avoid water colder than 4°C. Edwards (1965) noted that in the late fall most U. chuss had migrated from the inshore industrial fishing grounds when the water temperature dropped to 5°C.

Adult $U.\ chuss$ migrate inshore in the spring of the year. Smith (1898) reported $U.\ chuss$ to be abundant at Woods Hole in May or June but rare

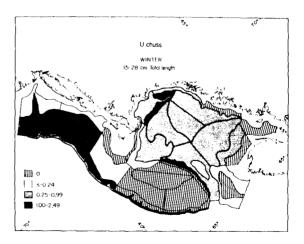


FIGURE 11.—Distribution and abundance of immature *Urophychis chuss* during the winter. Abundance in each sampling stratum is indicated on a log scale.

in the summer. Latham (1917) reported U. chuss from Orient, Long Island, in the spring but not summer. Breder (1922) noted U. chuss from Sandy Hook Bay in the spring; and Hildebrand and Schroeder (1928) reported that off New Jersey and New York U. chuss appeared in April, distended with spawn, that they remained close inshore for a short period, were caught 2 to 6 miles off until late May, and in July were abundant offshore on Cholera Bank. Edwards and Lawday (1960) reported that U. chuss were abundant in the industrial fish landings in April and May from the shallow inshore fishing grounds off No Man's Land, Mass., and Point Judith, R.I. The fish dispersed in June and July and were less available to the fishery.

After they migrate inshore in the spring, southern New England *U. chuss* migrate offshore in the summer to spawn. Mature *U. chuss* were heavily concentrated during the summer (Figure 13) in the strata shoaler than 60 fm off Block Island and on the southwest part of Georges Bank.

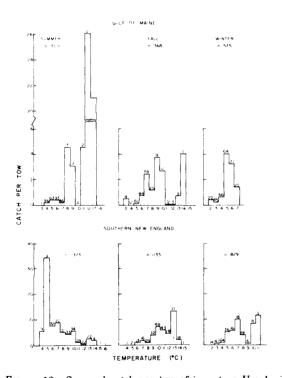


FIGURE 12.—Seasonal catch per tow of immature *Urophycis chuss* taken off southern New England and the Gulf of Maine. Abundance data are stratified by temperature intervals of one degree (C). The total number of individuals captured during each season = n. The number of stations occupied at each temperature is indicated above each respective histogram bar.

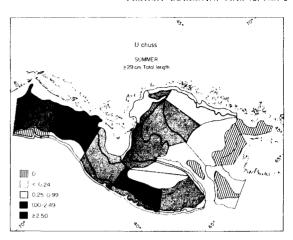


FIGURE 13.—Distribution and abundance of mature *Urophycis* chuss during the summer. Abundance in each sampling stratum is indicated on a log scale.

These concentrations were probably spawning aggregations because ripe fish were taken quite frequently during the survey (Musick, 1969). Also Domanevsky and Nozdvin (1963) reported spawning aggregations of U. chuss offshore on Georges Bank in July and August. Although a small number of U. chuss remain in the southern New England sounds during the summer (Edwards and Lawday, 1960), these are probably immature fish because spawning does not occur there. Wheatland (1956) found no U. chuss eggs or larvae in Long Island Sound, and Merriman and Sclar (1952) took no eggs but captured larvae in Block Island Sound, an area less land-locked and more adjacent to deep water than the previous one.

U. chuss emigration from shallow southern New England waters to offshore spawning grounds is probably correlated with temperature. Figure 14 shows that U. chuss were not abundant within adequately sampled temperature intervals higher than 12°C. Riley (1956) noted that temperatures exceeded 12°C over most of Long Island Sound during June and increased until October when temperatures were in excess of 20°C. Edwards, Livingstone, and Hamer (1962) reported that during the summer off southern New England U. chuss were most abundant at about 9°C, and Edwards (1965) showed that U. chuss migrated offshore when the bottom temperature reached about 10°C in the early summer.

In the Gulf of Maine *U. chuss* became available to the shallow water trawl fishery off Gloucester and Ipswich, Mass., in April or May

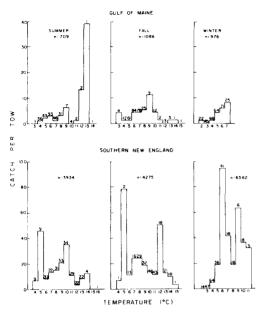


FIGURE 14.—Seasonal catch per tow of mature Urophycis chuss off southern New England and the Gulf of Maine. Abundance data are stratified by temperature intervals of one degree (C). The total number of individuals captured during each season = n. The number of stations occupied at each temperature is indicated above each respective histogram bar.

(Edwards, 1958a; Edwards and Lawday, 1960) and increased in abundance until August. Thus mature U. chuss are abundant in the summer at depths less than 30 fm. The Albatross IV survey data (Figure 13) which show highest values of abundance in strata 60 fm and deeper are probably not indicative of the true summer distribution of *U. chuss*. Both the industrial fishery and region of greatest abundance in the Albatross IV survey are in the southwestern section of the Gulf, but the fishery and survey data were taken at different depths. Additional evidence that U. chuss congregate in the summer at depths less than 30 fm comes from Bigelow and Schroeder (1953). They noted that U. chuss spawns in the Gulf in the summer and that most eggs and larvae have been collected close to shore. Water temperatures inshore are comparable to those that occur in known offshore spawning areas of U. chuss off southern New England (5°-10°C). Similar temperatures also occur in deeper waters of the Gulf, but young *U. chuss* spawned in such areas would have little chance of finding Placopecten for shelter after descending because Placopecten is restricted to shoal areas of the Gulf (Dow and Baird, 1960). Therefore, there may be selection

for inshore spawning in the Gulf of Maine.

During the fall (Figure 15), mature *U. chuss* were dispersed over the entire survey area, but the original data (Musick, 1969) show that most individuals longer than 32 cm had moved into water deeper than 60 fm. The winter distribution pattern of mature *U. chuss* (Figure 16) shows that a very strong offshore movement occurred in water deeper than 60 fm, in the Gulf of Maine, and off southern New England. The fish were most heavily concentrated along the edge of the continental slope from the southwest part of Georges Bank to Hudson Canvon, Edwards et al. (1962) reported *U. chuss* to be most abundant in winter between 100 and 250 fm in their study area south of Nantucket. In addition, Edwards et al. (1962) found that *U. chuss* were "most abundant where the water temperature was between 47°F (8.3°C) and 50°F (10.0°C)," values which are within the range which adult hake were most abundant in the present study (5-12°C).

Juvenile and immature *U. chuss* occurred within a narrower temperature range than the adults. However, the latter were more concentrated within relatively narrow temperature limits. This implies that although adults may tolerate a wider range, they may prefer a narrower range than young fish do or, at least, are more mobile and can undertake longer and faster seasonal migrations, thus remaining within relatively narrower temperature limits throughout the year. Such behavior might allow the fish to maintain an optimal thermal environment for gonadal development, spawning, and feeding during various times of the year.

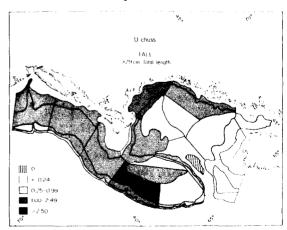


FIGURE 15.—Distribution and abundance of mature *Urophycis* chuss during the fall. Abundance in each sampling stratum is indicated on a log scale.

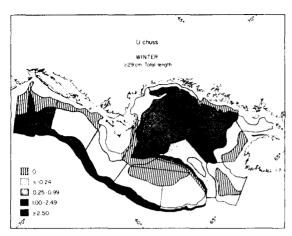


FIGURE 16.—Distribution and abundance of mature *Urophycis* chuss during the winter. Abundance in each sampling stratum is indicated on a log scale.

Seasonal Distribution of U. tenuis

During summer (Figure 17), immature *U. tenuis* were rare or absent over most of the southern New England area. Moderate numbers were taken in the strata deeper than 100 fm off Nantucket and the southern part of Georges Bank and the strata deeper than 60 fm along the eastern part of Georges Bank. In the Gulf of Maine, immature *U. tenuis* were taken in moderate numbers in the Great South Channel (Stratum 23) and in the northern part of the Gulf. The highest abundance value was in Stratum 39 off the northern Maine coast.

In the fall, immature *U. tenuis* were most abundant in the northern and eastern parts of the Gulf (Figure 18), and moderately abundant in the deep central Gulf, the Great South Channel, and on the middle and northern edge of Georges Bank. Immature *U. tenuis* were also abundant in the stratum deeper than 100 fm at the eastern edge of Georges Bank and moderately abundant in strata deeper than 60 fm to the south and west off southern New England. Only one stratum south of Georges Bank less than 60 fm deep (Stratum 2) had moderate numbers of *U. tenuis*. This stratum includes the inshore extension of Hudson Canyon.

In the Gulf of Maine during the winter (Figure 19), immature *U. tenuis* were most abundant in the deeper northern strata (Strata 36 and 38) and along the northern edge of Georges Bank. Immature *U. tenuis* were absent or rare in areas less than 60 fm off southern New England but

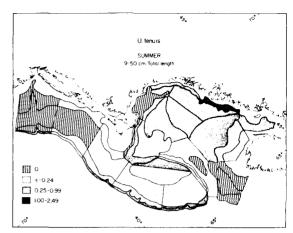


FIGURE 17.—Distribution and abundance of immature *Urophycis tenuis* during the summer. Abundance in each sampling stratum is indicated on a log scale.

were fairly abundant in some strata deeper than 100 fm

Indices of abundance of *U. tenuis* by temperature interval were less reliable than those of *U. chuss* because *U. tenuis* was much less abundant, particularly off southern New England. Single large tows often lowered the precision of mean catch estimates because of the relatively small total number of *U. tenuis* collected. Consequently, for some seasons only temperature ranges can be discussed. In the southern New England area, immature *U. tenuis* were taken from 4° to 14°C in the summer. Only one station was made at 15°C and at 16°C. Although *U. tenuis* was not taken there, the sampling

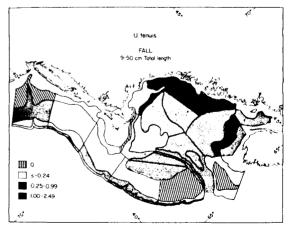


FIGURE 18.—Distribution and abundance of immature *Urophy*cis tenuis during the fall. Abundance in each sampling stratum is indicated on a log scale.

intensity does not give a true indication of its presence or absence. During the fall, immature U. tenuis occurred over the entire temperature range, 4° to 15°C. In the winter, they were taken from 3° to 10°C. In the Gulf of Maine in the summer, immature U. tenuis occurred from 4° to 9°C and the highest mean catch was at 8°C. The fish were absent at 3°C and from 10° to 14°C; however, these temperature intervals were not adequately sampled. In the fall, immature *U. tenuis* occurred from 3° to 11°C and the highest mean abundance was at 9°C. The fish were absent from 12° to 15°C but the sampling intensity at these temperatures was inadequate. In the winter, only a few fish were taken at 2°C and 3°C and mean catches increased from 4° to 7°C. Immature U. tenuis were taken over an annual range of 2° to 15°C but were most abundant between 4° and 10°C (Figure 20).

During the summer (Figure 21), mature *U. tenuis* were rare or absent off southern New England except in two strata deeper than 100 fm. They were moderately abundant in the Gulf of Maine and heavily concentrated in Stratum 39 along the northern coast of Maine. In the fall (Figure 22), off southern New England, mature *U. tenuis* were moderately abundant in all strata deeper than 100 fm, in two strata from 60 to 99 fm deep, and in only one stratum from 30 to 59 fm deep. They were rare or absent in all other southern New England strata. Mature *U. tenuis* were moderately abundant in the Gulf of Maine. The highest values of abundance are in Strata 27 and 28, between 60 and 100 fm.

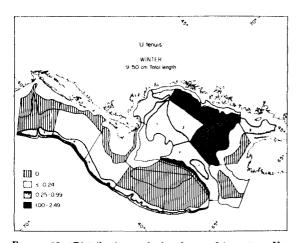


FIGURE 19.—Distribution and abundance of immature *Uro*phycis tenuis during the winter. Abundance in each sampling stratum is indicated on a log scale.

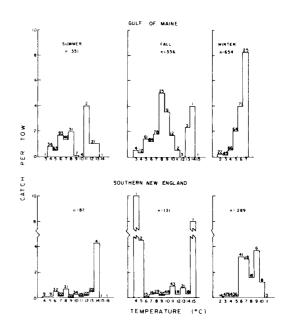


FIGURE 20.—Seasonal catch per tow of immature *Urophycis tenuis* off southern New England and the Gulf of Maine. Abundance data are stratified by temperature intervals of one degree (C). The total number of individuals captured during each season = n. The number of stations occupied at each temperature is indicated above each respective histogram bar.

During the winter off southern New England (Figure 23), mature *U. tenuis* were rare or absent in all strata shoaler than 100 fm except Stratum 7, which was 60 to 99 fm deep. Mature *U. tenuis* were moderately abundant there and in all strata deeper than 100 fm. In the Gulf of Maine, mature *U. tenuis* were absent from all strata

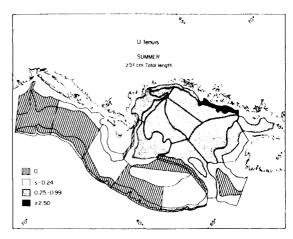


FIGURE 21.—Distribution and abundance of mature *Urophycis* tenuis during the summer. Abundance in each sampling stratum is indicated on a log scale.

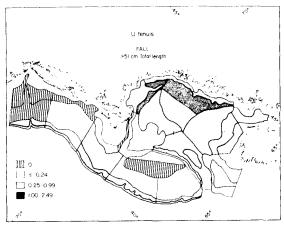


FIGURE 22.—Distribution and abundance of mature *Urophycis* tenuis during the fall. Abundance in each sampling stratum is indicated on a log scale.

shoaler than 60 fm. They were moderately abundant in most deeper strata and most abundant in Strata 28 and 36, which were deeper than 100 fm.

Catches of adult U. tenuis off southern New England were very small. Consequently, temperature-abundance estimates (Figure 24) are not reliable. Adult U. tenuis occurred from 6° to 12° C in the summer, from 4° to 13° C in the fall, and from 4° to 10° C in the winter. Adult U. tenuis were taken in the Gulf of Maine from 4° to 9° C in the summer (Figure 24). The highest mean catch was at 8° C. During the fall, the range of occurrence was 3° to 11° C, the highest mean catch occurring at 9° C, and in the winter the range was 2° to 7° C, the highest mean catch occurring at 7° C.

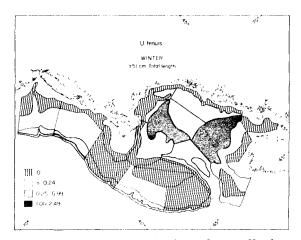


FIGURE 23.—Distribution and abundance of mature *Urophycis* tenuis during the winter. Abundance in each sampling stratum is indicated on a log scale.

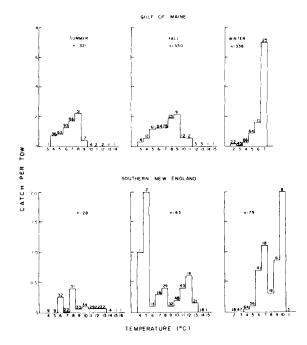


FIGURE 24.—Seasonal catch per tow of mature *Urophycis* tenuis off southern New England and the Gulf of Maine. Abundance data are stratified by temperature intervals of one degree (C). The total number of individuals captured during each season = n. The number of stations occupied at each temperature is indicated above each respective histogram bar.

Annually, adult U. tenuis were taken from 2° to 13° C but were most abundant between 5° and 9° C. Adult U. tenuis appear to occupy a more restricted temperature range than immature U. tenuis. Also, adult U. tenuis occupy a narrower and lower temperature range than adult U. chuss.

U. tenuis may be more abundant off southern New England than the survey data indicate. Edwards et al. (1962) and Schroeder (1955) frequently captured *U. tenuis* along the continental slope off southern New England at greater depths than those sampled during the *Albatross IV* survey and recent research (Musick, unpublished data) indicates that *U. tenuis* is a common member of the continental slope fish fauna of Virginia.

Distribution of *Urophycis chuss* and *U. tenuis* with Substrate

U. chuss and *U. tennuis* are absent or rarely occur on rock, shell, or gravel bottoms. Both "prefer" sand or mud. Few or no *Urophycis* occurred in Strata 24, 32, and 33 during any season.

These strata are dominated by rock or gravel bottoms (Fritz, 1965, Plate B). Storer (1858), Goode (1884), Hildebrand and Schroeder (1928), and Bigelow and Schroeder (1939) noted the association of *U. chuss*, *U. tenuis*, or both with mud bottoms. Bigelow and Welsh (1925) reported that both species dwelled over soft bottoms (silt. sand, or mud) but that the U. tenuis was more strictly a "mud fish" than the U. chuss. The Albatross IV data appear to agree with the last statement, because the regions where U. tenuis occurred most commonly are dominated by muddy or silty substrates—the northeastern Gulf of Maine, the central basins of the Gulf, and along the continental slope on Georges Bank and southwest. However, these areas are also cooler during the summer, and the correlation between U. tenuis abundance and mud bottoms (rather than sand) may be an artifact. Urophycis chuss were abundant over mud or sand or both depending on season, because the deeper strata were covered with muddy substrates whereas the shallower strata in the southwest Gulf of Maine and off southern New England were covered with sand (Fritz, 1965, Plate B).

ACKNOWLEDGMENTS

Thanks are due to R. L. Edwards and M. D. Grosslein of the National Marine Fisheries Service (NMFS) Laboratory, Woods Hole, Mass., for providing ship time, research space, and scientific direction during the course of my study. A. C. Kohler of the Fisheries Research Board of Canada Laboratory, St. Andrews, New Brunswick, provided me with specimens from the Gulf of St. Lawrence. G. Jónsson of the Hafrannsoknastofnunin Marine Research Institute, Reykjavik, sent me material from Iceland and D. M. Cohen of the NMFS Systematics Laboratory, Smithsonian Institution, allowed me to examine hake from Florida. Also, I wish to thank my students at the Virginia Institute of Marine Science—J. D. McEachran, K. Able, and C. Wenner-for collecting data for me on *Urophycis* while pursuing their own research at sea, and to G. W. Mead formerly of the Museum of Comparative Zoology, Harvard University, for thoroughly editing the early drafts of the dissertation from which parts of the present paper have been extracted. My research was supported in part by National Science Foundation grants G-19727 and GB-3167 to the Harvard Committee on Evolutionary Biology (Principal Investigator, Reed C. Rollins) and a Grant-in-Aid from the Sigma Xi - RESA Committee.

LITERATURE CITED

BIGELOW, H. B.

1927. Physical oceanography of the Gulf of Maine. Bull. U.S. Bur. Fish. 40(2):511-1027.

1933. Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. I. The cycle of temperature. Pap. Phys. Oceanogr. Meteorol. 4(1), 135 p.

BIGELOW, H. B., AND W. C. SCHROEDER.

1939. Notes on the fauna above mud bottoms in deep water in the Gulf of Maine. Biol. Bull. (Woods Hole) 76:305-324.

1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 576 p.

BIGELOW, H. B., AND W. W. WELSH.

1925. Fishes of Gulf of Maine. Bull. U.S. Bur. Fish. 40, 567 p.

BOURNE, N.

1964. Scallops and the offshore fishery of the Maritimes. Fish. Res. Board Can., Bull. 145, 60 p.

BREDER, C. M., JR.

1922. The fishes of Sandy Hook Bay. Zoologica (N.Y.) 2:330-351.

1948. Field book of marine fishes of the Atlantic coast. G. P. Putnam's Sons, N.Y., 332 p.

BULLIS, H. R., JR., AND J. R. THOMPSON.

1965. Collections by the exploratory fishing vessels Oregon, Silver Bay, Combat, and Pelican made during 1956 to 1960 in the southwestern North Atlantic. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 510, 130 p.

CORNISH, G. A.

1907. Notes on the fishes of Canso. Contrib. Can. Biol. 1902-1905:81-90.

1912. Notes on fishes of Tignish, Prince Edward Island. Contrib. Can. Biol. 1906-1910:79-81.

Cox, P.

1905. Extension of the list of New Brunswick fishes. Proc. Miramichi Nat. Hist. Assoc. 4:36-45.

1921. List of fishes collected in 1917 off the Cape Breton coast and the Magdalen Islands. Contrib. Can. Biol. 1918-1920:109-114.

Craigie, E. H.

1916. The life-history of the hake (Urophycis chuss Gill) as determined from its scales. Contrib. Can. Biol. 1914-1915:87-94.

1927. Notes on the total weights of squirrel hake, the pollock, the winter flounder, and the smelt, and on the weights of the liver and gonads in the hake and in the pollock. Trans. R. Soc. Can., Ser. 3, 21:153-173.

DICKIE, L. M.

1958. Effects of high temperature on survival of the giant scallop. J. Fish. Res. Board Can. 15:1189-1211.

Domanevsky, L. N., and Y. P. Nozdvin.

1963. Silver and red hakes. In Reproduction of fish stocks. AtlanNIRO, Fish Husbandry 39(5):10-13. (Engl. transl., P.S. Galtsoff, Bur. Commer. Fish. Woods Hole Lab., Ref. 63-8.) Dow, R. L., and F. T. Baird, Jr.

1960. Scallop resource of the United States Passamaquoddy area. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 367, 9 p.

EDWARDS, R. L.

1958a. Gloucester's trawl fishery for industrial fish. Commer. Fish. Rev. 20(8):10-15.

1958b. Species composition of industrial trawl landings in New England, 1957. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 266, 23 p.

1965. Relation of temperature to fish abundance and distribution in the southern New England area. Int. Comm. Northwest Atl. Fish., Spec. Publ. 6:95-110.

EDWARDS, R. L., AND L. LAWDAY.

1960. Species composition of industrial trawl-fish landings in New England, 1958. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 346, 20 p.

EDWARDS, R. L., R. LIVINGSTONE, JR., AND P. E. HAMER. 1962. Winter water temperatures and an annotated list of fishes—Nantucket shoals to Cape Hatteras. Albatross III Cruise no. 126. U.S. Fish Wildl. Serv., Spec. Sci. Rep Fish. 397, 31 p.

EDWARDS, R. L., AND F. E. LUX.

1958. New England's industrial fishery. Commer. Fish. Rev. 20(5):1-6.

FORTIN, P.

1863. List of the cetacea, fishes, crustacea and mollusca which now inhabit . . . the Canadian shores of the Gulf of St. Lawrence, etc. Annu. Rep. of Pierre Fortin, Esq., Magistrate in command of the Expedition for the Protection of Fisheries in the Gulf of St. Lawrence, during the seasons of 1861 and 1862. Append. 109-124. Quebec.

FRASER-BRUNNER, A.

1925. New or rare fishes from the Irish Atlantic slope. Proc. R. Irish Acad. 43:319-326.

FRITZ, R. L.

1965. Autumn distribution of groundfish species in the Gulf of Maine and adjacent waters, 1955-1961. Ser. Atlas Mar. Environ. Folio 10, 1 p.

GILPIN, B. J.

1867. On the food fishes of Nova Scotia, No. 5, the cod family. Proc. Trans. N. S. Inst. Nat. Sci. 2(1):101-111.

GOODE, G. B.

1884. Natural history of useful aquatic animals. Part III, The food fishes of the United States. In G. B. Goode, Fisheries and fishery industries of the U.S., Sec. I:163-682.

GROSSLEIN, M. D.

1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-30.

HILDEBRAND, S. F., AND W. C. SCHROEDER.

1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43(1), 366 p.

JORDAN, D. S., AND B. W. EVERMANN.

1898. The fishes of North and Middle America. Part III. U.S. Natl. Mus. Bull. 47:2183-3136.

KENDALL, W. C.

1909. The fishes of Labrador. Proc. Portland Soc. Nat. Hist. 2:207-243.

KNIGHT, T. F.

1866. Descriptive catalogue of the fishes of Nova Scotia. Halifax. 54 p.

LATHAM. R.

1917. Migration notes of fishes, 1916, from Orient, Long Island. Copeia 41:17-23.

LEIM, A. H., AND W. B. SCOTT.

1966. Fishes of the Atlantic coast of Canada. Fish Res. Board Can., Bull. 155, 485 p.

MCKENZIE, R. A.

1959. Marine and freshwater fishes of the Miramichi River and Estuary, New Brunswick. J. Fish. Res. Board Can. 16:807-833.

MERRIMAN, D., AND R. C. SCLAR.

1952. The pelagic fish eggs and larvae of Block Island Sound. Bull. Bingham Oceanogr. Collect., Yale Univ. 13(3):165-219.

MOYLE, J. B., AND R. LOUND.

1960. Confidence limits associated with means and medians of series of net catches. Trans. Am. Fish. Soc. 89:53-58.

Musick, J. A.

1969. The comparative biology of two American Atlantic hakes, *Urophycis chuss* and *U. tenuis* (Pisces, Gadidae). Ph.D. thesis, Harvard Univ., Cambridge, Mass., 150 p.

1973. A meristic and morphometric comparison of the hakes, *Urophycis chuss* and *U. tenuis* (Pisces, Gadidae). Fish. Bull., U.S. 71:479-488.

NEWFOUNDLAND FISHERIES RESEARCH COMMISSION.

1932. First list of fishes in the Newfoundland fishing area. Newfoundland Fish. Res. Comm., Annu. Rep. 1(4):107-110.

1933. Second list of fishes in the Newfoundland fishing area. 1932. Newfoundland Fish. Res. Comm., Annu. Rep. 2(1):125-127.

1934. Third list of fishes in the Newfoundland fishing area. 1933. Newfoundland Fish. Res. Comm., Annu. Rep. 2(2):115-117.

PEREYRA, W. T., H. HEYAMOTO, AND R. R. SIMPSON.

1967. Relative catching efficiency of a 70-foot semiballoon shrimp trawl and 94-foot eastern fish trawl. U.S. Fish. Wildl. Serv., Fish. Ind. Res. 4(1):49-71.

RILEY, G. A.

1956. Oceanography of Long Island Sound, 1952-1954.
 II. Physical oceanography. Bull. Bingham Oceanogr.
 Collect., Yale Univ. 15:15-46.

Roessler, M.

1965. An analysis of the variability of fish populations taken by otter trawl in Biscayne Bay, Florida. Trans. Am. Fish. Soc. 94:311-318.

SCHROEDER, W. C.

1955. Report on the results of exploratory otter-trawling along the continental shelf and slope between Nova Scotia and Virginia during the summers of 1952 and 1953. Pap. Mar. Biol. Oceanogr., Deep-Sea Res., suppl. to Vol. 3, p. 358-372.

SMITH, H. M.

1898. The fishes found in the vicinity of Woods Hole. Bull. U.S. Fish Comm. 17:85-111.

STORER, D. H.

1839. A report on the fishes of Massachusetts. Boston J. Nat. Hist. 2:289-570.

1846. A synopsis of the fishes of North America. Mem. Am. Acad. Arts Sci., New Ser. 2:253-550.

1858. A history of the fishes of Massachusetts. Mem. Am. Acad. Arts Sci., New Ser. 6:309-371.

STORER, H. R.

1850. Observations on the fishes of Nova Scotia and Labrador, with descriptions of new species. Boston J. Nat. Hist. 6(1):247-270.

SVETOVIDOV, A. N.

1955. Notes on *Phycis borealis* Saemundsson (Pisces, Gadidae). Tr. Zool. Inst. Acad. Nauk. SSRF 17:346-348.
(Engl. transl., [U.S.] Bur. Commer. Fish., Ichthyol. Lab., Wash., D.C., 1961, 6 p.)

TAYLOR, C. C.

1953. Nature of variability in trawl catches. U.S. Fish Wildl. Serv., Fish. Bull. 54:145-166.

TEMPLEMAN, W.

1966. Marine resources of Newfoundland. Fish. Res. Board Can., Bull. 154, 170 p.

VLADYKOV, V. D., AND D. E. MCALLISTER.

1961. Preliminary list of marine fishes of Quebec. Nat. Can. 88:53-78.

VLADYKOV, V. D., AND R. A. MCKENZIE.

1935. The marine fishes of Nova Scotia. Proc. N.S. Inst. Sci. 19:17-113.

VLADYKOV, V. D., AND J. L. TREMBLAY.

1935. Liste des poissons recuellis pendant l'été 1934 par la Station Biologique due St. Laurent, dans la région de Trois-Pistoles, P.Q. Nat. Can. 62:77-82.

WHEATLAND, S. B.

1956. Oceanography of Long Island Sound, 1952-1954.
VII. Pelagic fish eggs and larvae. Bull. Bingham Oceanogr. Collect., Yale Univ. 15:234-314.